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TOWARDS A REVISION OF THE *RUDBECKIA FULGIDA* COMPLEX (ASTERACEAE), WITH DESCRIPTION OF A NEW SPECIES FROM THE BLACKLANDS OF SOUTHERN USA

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ABSTRACT

Taxonomy of the *Rudbeckia fulgida* Ait. complex is reviewed, resulting in description of a new species, **Rudbeckia terranigrae** J.J.N. Campbell & Seymour, **sp. nov.**, and notes on other poorly understood taxa. This species is known mostly from the Black Belt and Jackson Prairie regions of Alabama and Mississippi. However, it appears closely related to a few outlying collections from southwest Missouri and central Texas, plus a larger group of collections centered in the cedar glade region of Tennessee, which could include another undescribed species. *Rudbeckia terranigrae* and these other plants are southern relatives of previously described taxa with more central or northern ranges in eastern states, especially *R. tenax* and *R. speciosa* sensu stricto. Appropriate taxonomic treatment for all of these plants remains uncertain, but their morphology and biogeography suggests that they should not be simply combined with *R. fulgida* sensu stricto, which is largely restricted to southern Appalachian regions, the Piedmont, and mid-Atlantic Coastal Plain. They all produce stoloniferous offsets after flowering, their paleae are generally eciliate or weakly ciliate at apices, and they tend to occur on calcareous substrates. In contrast, typical *R. fulgida* and its closest relatives do not produce elongated offsets, their paleae have ciliate apices, and they usually occur on non-calcareous substrates.

A provisional key to all taxa within the *fulgida* complex is presented, with three subgroups. (1) *Rudbeckia truncata* and *R. missouriensis* have relatively narrow leaves without distinct petioles, paleae glabrous or nearly so, and a lack of stoloniferous offsets. They typically occur on somewhat xeric sites near calcareous outcrops. (2) The *fulgida-tenax* subgroup (including *R. speciosa* and *R. terranigrae*) have largest basal and lower cauline leaves with petioles ca. 2–12 cm long and blades cuneate, ca. 2–8 × 1–5 cm; mid-cauline leaves are shallowly dentate to almost entire (except for irregular lacerations), the regular teeth usually no more than 1(–2) mm deep; outer paleae often have distinctly thickened waxy apices; rays number ca. 6–14 and are mostly 1–2.5 cm long. These species typically occur in grassy openings that are maintained by disturbance rather than just xeric or hydric extremes. (3) The *umbrosa-palustris* subgroup (including *R. chapmannii*, *R. sullivantii*, and *R. deamii*) have largest basal and lower cauline leaves with ca. 12–30 cm petioles, their blades broadly cuneate, truncate or subcordate, ca. 8–15 × 3–10 cm; mid-cauline leaves are often coarsely dentate with teeth at least 2 mm deep; outer paleae usually lack thickened waxy apices; rays number ca. 12–21 and are mostly 1.5–3 cm long. These species occur typically on mesic to hydric sites, especially in calcareous seeps, fens, or similar habitats.

KEY WORDS: Asteraceae, *Rudbeckia fulgida* complex, blacklands, Mississippi, Alabama.

Rudbeckia contains about 20–30 species, all native to North America and concentrated in the southeastern USA. Several taxa are rare to endangered, with small ranges and restricted habitats. The genus has also become widely known in Europe and elsewhere through introductions for horticultural interest. Several species or species complexes contain significant variation that has been hard to describe in traditional taxonomic terms. *Rudbeckia fulgida* Ait. and its allies form a complex of taxa that has been particularly difficult to understand and variously treated (e.g., Small 1903, 1933; Fernald 1950; Perdue 1957; Cronquist 1980; Urbatsch & Cox 2006; Weakley 2012).

This paper is derived from general observations on the *fulgida* complex in the field, herbarium, and garden during the last 30 years. During the 1980s, some botanists in Kentucky realized that at least two described taxa in the state had been generally ignored within published treatments after 1950: *Rudbeckia tenax* C.L. Boynt. & Beadle and *R. truncata* Small (e.g., Palmer-Ball et al. 1988; Cranfill 1991; Medley 1993). Subsequent investigations across southeastern states confirmed the need for a reassessment of the *fulgida* complex. The 'last straw'—prompting publication now—was the recent discovery of an undescribed species in Mississippi, as reported below. Note, however, that much deeper analysis is still needed, with investigation of cytology, molecular characters, and comparative ecology. This paper will hopefully stimulate such work.

OUTLINE OF THE *RUDBECKIA FULGIDA* COMPLEX

The complex belongs to *Rudbeckia* sect. *Rudbeckia*, which is concentrated in the eastern half of the USA. (Urbatsch & Cox 2006). Some taxa of this section extend further west (especially those of the *R. hirta* complex), and a few occur in Mexico or Canada. The other major section of the genus, sect. *Macrocline* Torr. & Gray, is more wide-ranging. Distinctive characters of sect. *Rudbeckia*, as compared to sect. *Macrocline*, include these: pappus coronoid [toothed] or glandular or lacking (versus coronoid); cypselae [fruits] smaller, ca. 1.5–3.5 mm long (versus 3.5–7.5 mm in most taxa), exceeded (versus not exceeded in most taxa) by their paleae [receptacular bracts]; receptacles usually hemispheric to conic (versus conic to columnar in most taxa); disc corollas somewhat brownish-purple, at least distally (versus light to reddish brown, at least proximally, sometimes greenish to yellow distally); laminae of ray corollas often becoming orange to maroon in proximal third or more, at least when dried (versus remaining uniformly bright yellow); leaves and stems not strongly glaucous (versus usually glaucous).

Reported chromosome numbers in *Rudbeckia*, broadly defined, appear to be based on x = 16, 18, or 19. Reported full complements (2n) are 32 (only in *R. amplexicaulis* Vahl), 36, 38, 54, 57, 72, 76, and 102 (Perdue 1959; Urbatsch & Cox 2006; Palmer et al. 2009). Also, occasional aneuploids have been found in the *fulgida* complex (Perdue 1959) and in the *hirta* L. complex (Palmer et al. 2009). Numbers above 2n = 38 occur mostly in taxa with relatively large or divided lower leaves, including *R. triloba* L. and *R. laciniata* L. Such taxa occur in relatively mesic or subhydric habitats, where denser ground vegetation may have selected plants with more capacity to change their foliar architecture, from basally-concentrated coverage early in the season to taller flowering stems later in the season. Within sect. *Rudbeckia* reported numbers are mostly 2n = 38 or 76, but some forms of *R. triloba* have ca. 57. In contrast, numbers for sect. *Macroline* are mostly 2n = 36, but some forms of *R. laciniata* have 54, 72, 102, or perhaps more. Both *R. triloba* and *R. laciniata* may be largely apomictic in their reproduction from seed (Gustafsson 1947).

Palmer et al. (2009) recently showed that within sect. *Rudbeckia* there are large, characteristic differences in DNA content between species, independent of chromosome number, suggesting "recent and substantial changes in genome size." They found that these plants are generally self-incompatible in pollination, as also reported by Scott and Molano-Flores (2007). However, small numbers of seed were produced in some cases through apomixis (pseudogamy, especially after interspecific pollen reception) or perhaps even rarer self-pollination. Artificial interspecific crosses generally fail but

have been successful in two reported cases: "*fulgida*" × *missouriensis* (McCrea 1981); and "*hirta*" × *subtomentosa* (Palmer et al. 2009). Perdue (1957) noted that "No plants have been observed in the herbarium or in the course of extensive field work that offer even the most remote suggestion of interspecific hybridization." However, he adopted broad definitions of both *R. fulgida* and *R. hirta*. In a pioneering survey of ribosomal DNA, King and Schaal (1989) showed that *R. missouriensis* has relatively little variation within or between populations, which they noted might be attributed to a 'founder effect' in colonization of its fragmented habitat patches.

Rudbeckia fulgida and its close relatives form the core of sect. *Rudbeckia*, together with *R. grandiflora* (D. Don.) J.F. Gmel. ex DC, *R. heliopsidis* Torr. & Gray, *R. subtomentosa* Pursh, and *R. triloba*. The other species placed by Urbatsch and Cox (2006) in sect. *Rudbeckia* are the *R. hirta* complex (including *R. serotina* Nutt. and several other potential segregates), *R. mollis* Elliott, and *R. graminifolia* (Torr. & Gray) C.L. Boynt. & Beadle. Morphological characters that together generally distinguish the *fulgida* complex within sect. *Rudbeckia* are as follows: perennials, ca. 0.5–1.5 m tall; larger leaf blades ca. 5–15 cm long, unlobed, not amplexicaul, not gland-dotted; heads 1–7(–12+) in loose corymbiform arrays; paleae rounded to acute but not cuspidate, their outer surfaces glabrous to pilose but not canescent or strigose. Small (1933) divided species of the *fulgida* complex into ser. *Fulgidae* and ser. *Speciosae*, but series within the genus have not been adopted by subsequent authors. The currently reported distribution of *R. fulgida* sensu lato (Kartesz 2010; Fig. 1) reveals a number of somewhat disjunct populations, which are detailed further below.

As in most species of sect. *Rudbeckia*, a feature of the *fulgida* complex is the tendency for at least proximal sections of ligules [in ray florets] to turn orange or maroon (as in *R. graminifolia*), especially when matured and dried. Moreover, disc corollas, paleae, phyllaries, and stems often dry to a somewhat orange, reddish, or purplish hue, versus simply yellowish-brown [stramineous]. This 'orangeness' deserves investigation at the molecular level. It tends to be less clearly visible to human eyes in flowers of the highly variable *R. hirta* complex (Palmer et al. 2009) and in *R. mollis*, though cryptic ultraviolet patterns can often occur as well or instead (Abrahamson & McCrea 1977; McCrea 1981; McCrea & Levy 1983). The *R. hirta* complex and *R. mollis* are also distinct from the rest of sect. *Rudbeckia* in the hirsute-hispid apices of their paleae (with relatively dense, long, multicellular hairs up to ca. 0.5 mm) and in their generally annual to biennial, tap-rooted growth form, which may be a factor in their general exclusion from damp soils by diseases or other factors. All other taxa in sect. *Rudbeckia* are perennials with branching caudices or, in some cases, rhizomes or stolons.

Based on morphology, it may be reasonable to ally Small's ser. *Graminifoliae* with the *fulgida* complex. But that pair of species—*Rudbeckia graminifolia* and *R. mohrii* Gray—have extraordinarily long narrow graminoid leaves and probably other distinctive features. They are typical of damp southeastern pinelands and ponds. Urbatsch and Cox (2006) placed *R. mohrii* in sect. *Macrocline* based partly on reported chromosome numbers, though it seems somewhat transitional, with cypselae (seeds) only 3.4–4.2 mm long and an "ovoid or ellipsoid to hemispheric" receptacle.

Other somewhat anomalous species that have appeared superficially similar to the *fulgida* complex include *Rudbeckia auriculata* (Perdue) Kral and *R. scabrifolia* L.E. Brown. Both species have small ranges, in Alabama-Georgia-Florida and Louisiana-Texas respectively. Chromosome numbers and other characters support their placement in sect. *Macrocline* (Urbatsch & Cox 2006), but further investigation is warranted. Compared to more typical members of sect. *Macrocline*, they have smaller seeds, receptacles are not strongly columnar, and leaves do not appear particularly glaucous. Their mid-stem leaves tend to have auriculate bases, especially those of *R. auriculata*. Such leaves are rare in the genus but pronounced in *R. amplexicaulis* Vahl, which is an annual placed by itself in sect. *Dracopis* (Cass.) Gray or sometimes treated as a monotypic genus.

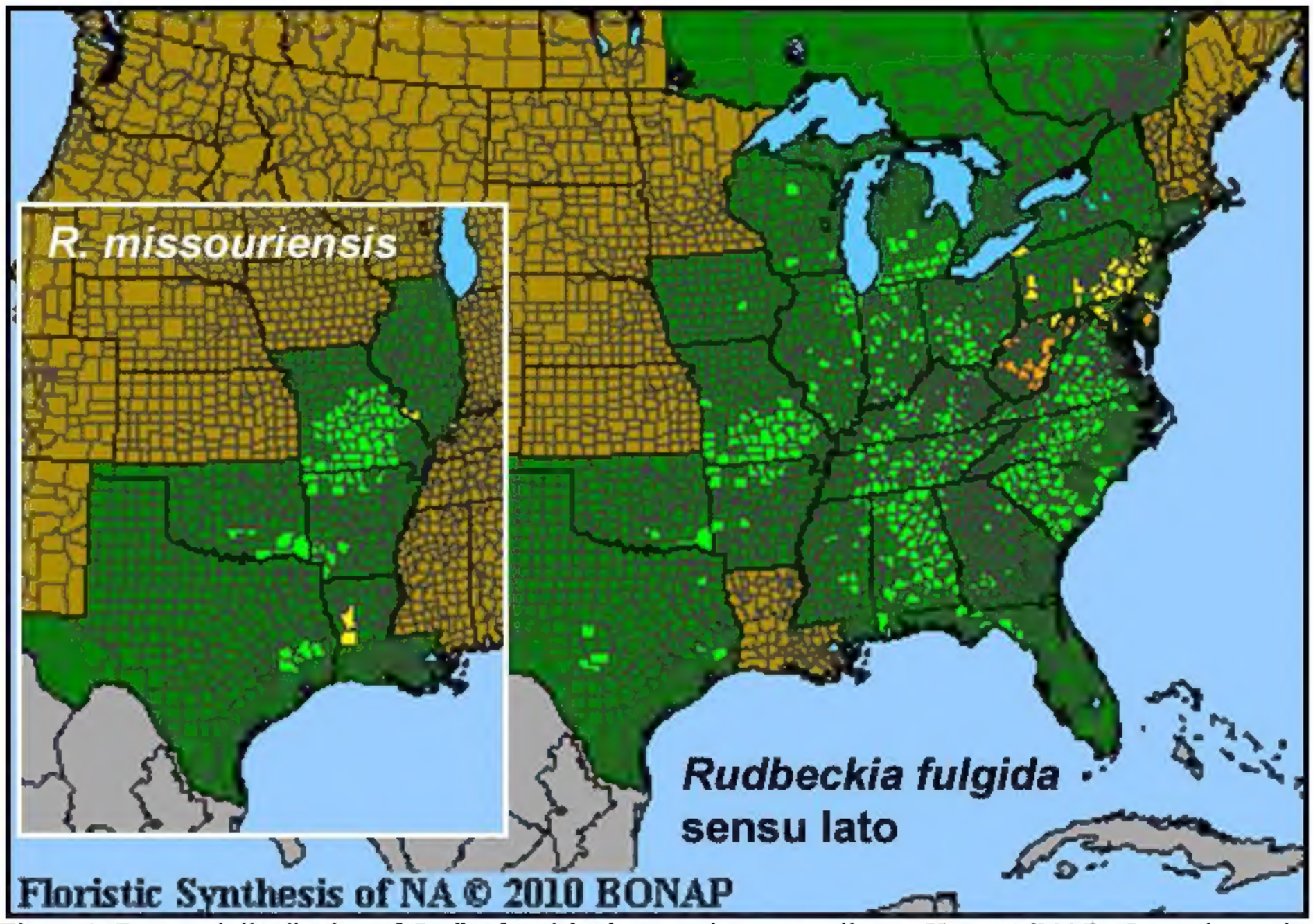

Figure 1. Reported distribution of *Rudbeckia fulgida* sensu lato, according to Kartesz (2010). Inset shows the distribution of *R. missouriensis*, the only member of the *fulgida* complex separated in the Kartesz data. Dark green indicates presence in the state; light green indicates presence in the county. In states with recorded counties colored yellow or orange, the species is considered imperiled or locally extinct. See also NatureServe (2013), which indicates vulnerable to imperiled status in West Virginia, Pennsylvania, Maryland, Delaware, and Ontario, but exotic status in Quebec.

A NEW SPECIES FROM THE BLACKLANDS OF SOUTHERN STATES

We became aware of this species during field work at the Pulliam Prairie in Chickasaw County and elsewhere in the Black Belt of Mississippi (Campbell & Seymour 2012 and in press). Several additional collections were discovered in herbaria, usually under the name *Rudbeckia fulgida*.

RUDBECKIA TERRANIGRAE J.J.N. Campbell & Seymour, **sp. nov.** Figs. 2, 3. **TYPE: USA. Mississippi.** Chickasaw Co.: Pulliam Prairie, ca. 1 mi NE of Buena Vista (intersection of County Roads 402 and 406), locally common at lower edges of grassland, often in transitions to riparian thickets and edges, 22 Aug 2009, *W.R. Seymour & J.J.N. Campbell 390* (holotype: MISS). Paratype from same locality, 23 Aug 2009, *W.R. Seymour & J.J.N. Campbell 427* (MISS). In addition, material from cultivation of these plants has been collected for APSC (18 Sep 2013, *J.J.N. Campbell s.n.*) and NY (20 Sep 2012, *J.J.N. Campbell s.n.*).

Similar to *Rudbeckia tenax* C.L. Boynt. & Beadle in its paleae mostly eciliate, discs of primary heads averaging ca. 12–16 mm wide, plants with distinct stoloniferous offsets (2–)3–10 cm long, and leaves up to 3–5(–7) cm wide, but different from it in the heads opening mostly during early August to mid-September, often solitary or with one distinctly larger (versus opening more or less together mostly during mid-July to mid-August, with 2–7), midcauline leaves mostly 1.5–4.5 cm wide, with length/width 3–6, their distinct petiolar bases mostly 4–8 mm wide with almost parallel sides (versus 0.5–2.5 cm wide, with length/width 4–10, tapering to less distinct petiolar bases mostly

2–4 mm wide), stems and leaves thinly to densely rough-hirsute with mostly spreading pustulate hairs (vs. thinly to densely pilose with mostly appressed soft hairs).

Perennial herbs ca. 40–90 cm tall, with stoloniferous offsets extending ca. 5-10 cm. **Stems** hispid or hirsute with spreading hairs mostly 1–2.2 mm long, densely so and usually antrorse in the inflorescence but thinly so to glabrate below, where often retrorse. **Leaves** somewhat bluish green, shallowly dentate (especially in distal ¾) to almost entire (especially in proximal ¼), roughly strigose-hirsute above with 0.2–1.3 mm hairs, roughly hirsute below, especially along veins, with 0.7–1.8 mm hairs. **Lower leaves** (on lower ⅓ of stem and in tufts terminating offsets) with blades broadly ovate to elliptic, (6–)8–11 × (2–)2.5–3.5 cm, bases cuneate, petioles (3–)5–8 cm long, with little or no winged margin. **Midstem leaves** (below inflorescence) 6–17 × 2–4.5 cm, with length/width ca. 3–4.5, usually ascending and forming an overlapping (when pressed) cluster of 6–12 along 10–15 cm of stem, the petioles winged, 4–8(–12) mm wide, mostly parallel-sided except for the slightly flared base. **Upper leaves** (on inflorescence branches) 1.5–7 × 0.5–3 cm. **Heads** 1–6(–12) in open corymbiform arrays, usually solitary at first in mid-August, but often adding lateral ones until mid-September. **Phyllaries** 9–14(–20) × 1.5–4(–7) mm, sparsely to densely hispid, especially towards base, blunt to acute, usually mucronate with a distinct white-waxy point. **Receptacles** slightly rounded to hemispheric, 3–6 mm high × 8–13 mm wide. **Paleae** 3.5–5 × 1–1.5 mm, apices acute with pale waxy point, entire to slightly erose, largely eciliate (at least on apices), glabrous or sparsely strigose on both surfaces. **Ray florets** 9–13, laminae oblanceolate, mostly 16–23 × 3.3–6 mm, retuse, thinly strigose on backs. **Disc florets** ca. 300–500, corollas proximally yellowish-green (drying stramineous), distally brownish-purple (drying blackish), 3.2–3.9 mm. **Style branches** 1.1–1.3 mm, apices rounded. **Cypselae** 2.1–2.5 mm. **Pappus** slightly coroniform, lobes up to 0.2 mm.

Flowering usually in early August to mid-September. Low edges of blackland prairies, adjacent thickets and thin riparian to swampy woods, usually along sunny edges of riparian thickets or brushy swales, where potentially competing tall grasses (such as *Tripsacum dactyloides*, *Andropogon gerardii*, and *Sorghum halepense*) have been reduced by browsing, burning, plowing, or other disturbance. Alabama, Mississippi, and Tennessee (Fig. 4). Most records are from the Black Belt on Cretaceous chalk, in Alabama, Mississippi, and one locality in Tennessee. Other records are from the Jackson Prairie of southern Mississippi, on Eocene chalk, where plants tend to be larger with less glaucous, darker green foliage. The plant from Tennessee deserves further analysis, since it appears to be tetraploid based on flow cytometry; in cultivation it appears more robust, with longer hairs on stems and with basal offsets that are more superficial (vs. distinctly buried). *Rudbeckia terranigrae* is named after the 'blacklands' of southeastern states that are concentrated on the Gulf Coastal Plain. The sticky 'hydroxeric' vertisols of blacklands form a characteristic component of the habitats for these plants (Peacock & Schauwecker 2003; Campbell & Seymour 2011a, b).

Additional collections examined are as follows [brackets contain notes of the senior author]. **USA. Alabama.** Barbour Co.: roadside of Silo Rd, 2.1 mi N of Hwy 82 in Comer, small colony in woods near creek, 3 Oct 1998, *J.R. MacDonald 12147* (IBE). Butler Co.: County Hwy 7, 1 mi S of the Lowndes Co. line, thin soil on limestone outcrop, 6 Sep 2007, *A.R. Diamond 18042* (TROY); State Hwy 263, 2.1 mi S of the Lowndes Co. line, blackbelt, 12 Aug 2010, *A.R. Diamond 21531* (TROY). Dallas Co.: chalk prairie by US 89 10 mi W of Selma, 6 Oct 1972, *R. Kral 48840* (TENN). Hale Co.: jct. hwy 69 and county road 25, open roadside ditch, sunny chalky prairie soil, common, 24 Sep 1965, *S.E. Maginniss 100* (UNA); just N of Newbern on State Hwy 61, heavy earth prairie, 4 Sep 1969, *R. Kral 36868* (GA, IBE) [unusually robust with 8 heads, petiolar bases up to 12 mm wide]. Lowndes Co.: ca. 0.5 mi NW of Letohatchee on State Hwy 97, ca. 250 m NW of the intersection with County Hwy 37, 2.2 mi NW from Exit 151 of I-65, 9 Sep 2004, *C.J. Hansen 1628* (TROY). Marengo Co.: ca. 3 mi S of Demopolis along US 43, outcrop of Demopolis Chalk, 7 Oct 1967, *R. Kral 29620* (NCU, TENN); chalk outcrop area 0.7 mi WSW of Demopolis, 9 Sep 1968, *R. Kral 33107* (NCU). Montgomery Co.: roadsides near Montgomery, rare [in] central districts, 25 Aug 1885, *Geological Survey 802 [C.T. Mohr]* (UNA); roadside near Montgomery, 26 Aug 1885, *J.D. Smith 457* (US); intersection of county

hwys 18 and 39, blackbelt, *A.R. Diamond 21541* (TROY, UWAL). Sumter Co.: 4 mi S of Livingston, chalk outcrop, common in low moist areas, 31 Jul 1968, *J.L. Thomas 1765* (UNA); Old Bluffport, 11 Sep 1993, *L. Stanton B-22* (UWAL). Wilcox Co.: roadside, Lower Coastal Plain substation – Camben, 29 Aug 1960, *S.B. Jones & C.A. Jones 373* (NCU). **Mississippi**. Alcorn Co.: along State Hwy 2 just S of junction with US 72, calcareous area, 22 Aug 1967, *L.C. Temple 6593* (GA, MISS) [leaves somewhat glaucous below]. Clay Co.: Kilgore Hills area, 6 mi NE of Montpelier, Demopolis Formation, dense colony on edge of corn field, 2.5 ft tall, 18 Aug 1967, *T.R. Simmons CL-549* (MMNS); Hwy 47 N of West Point, 5 mi N of junction with Hwy 50, open prairie on chalk outcrop, common, 9 Sep 1968, *J.L. Thomas 1787* (NCU, UNA); ca. 5.5 mi NE of Montpelier, lowland prairie over Demopolis Chalk under *Juniperus virginiana*, 23 Aug 1978, *K.L. Gordon 617* (MMNS); Kilgore Hills, calcareous rocky areas in cedar barrens, 21 Aug 1978, *K.E. Rogers 45641* (TENN); Kilgore Hills, prairie and barrens, 23 Aug 1978, *K.E. Rogers 45623* (TENN). Jasper Co.: 3 mi SW of Rose Hill, sticky clay alkaline soil of Jackson Prairie, full sun with *Vernonia, Solidago, Helianthus, Ambrosia, Andropogon* and *Desmodium*, 8 Sep 1967, *S.B. Jones 15179* (GA, IBE, NCU); Tallahala Wildlife Management Area, ca. 2 mi S of intersection of State Rd. #505 with USFS #506, along USFS #507-A, low moist area along floodplain of small stream under thin somewhat open canopy, 18 Aug 1988, *D.T. Carraway 259* (IBE, MMNS). Monroe Co.: DeMoville Tract, centered at 33 55' 60" N 88 38' 37" W, ca. 1 mi WSW of Herndon Lane at McAllister Rd, on terrace of Mattubby Creek in thin swampy woods dominated by oaks, ashes and hickories, 8 Jun [non-flowering] & 29 Jul [flowering] 2010, *R. Seymour & J. Campbell 2142, 2197* (MISS). Newton Co.: ca. 2 mi E of Lake, Jackson Prairie Belt, open hog wallow prairie surrounded by loblolly pine, Eutaw-Vaiden Clay, stoloniferous, 16 Aug 1978, *K.L. Gordon 587 & 592* (MMNS); grassy field in Black Prairie region 3 mi E of Lake, 27 Jul 1956, *J.D. Ray 7262* (NCU). Oktibbeha Co.: ca. 4 mi NE of Starkville, roadside of Old Westpoint 0.3 mi E of junction with 16th Section Rd, occasional, 23 Sep 1995, *J.R. MacDonald et al. 9164* (IBE, UNA). Pontotoc Co.: ca. 4 mi ESE of Chiwapa, prairie remnant on edge of cropland, with frequent *Ratibida, Petalostemum, Andropogon, Rudbeckia, Liatris, Lobelia*, 5 Aug 1980, *K.L. Gordon 2113 with J. Burris* (IBE, MMNS). Scott Co., Harrell Prairie Hill 2.5 mi SE of Forest, full sun, sticky prairie soil. 9 Sep 1969, *S.B. Jones et al. 17828* (GA, IBE); ca. 3 mi SE of Forest, Bienville National Forest, Harrell Prairie Hill, open prairie on hills side, black prairie soil on the Jackson Formation, Yazoo Clay Member [and/or Moody's Branch Marl Member], stoloniferous, 13 Jul 1978, *K.L. Gordon et al. 416*; same locality, 16 Aug 1978, *K.L. Gordon et al. 569 & 570*; same locality, 7 Aug 1979, *K.L. Gordon 1340 & 1341* (MMNS). Scott Co.: 1 mi S of Forest on Highway 501 then 2 mi E on USFS 518, Harrell Prairie Hill Botanical Area, site 1-1, 550 ft elevation, tall grass prairie dominated by *Schizachyrium scoparium* and *Sorghastrum nutans*, highly calcareous soil inhibits pine growth, 26 Jul 1990, *R.G. Wieland 6323* (MMNS); Circle Prairie, Compartment #75 USFS Bienville National Forest, 450 ft elevation, small circular prairie opening burned past winter/spring, calcareous soils inhibit pine growth, small colony at edge of prairie, 13 Sep 1994, *R.G. Wieland 6814* (MMNS). Wayne Co.: scattered on small limestone glade, S of Coldwater Creek and W of Tokio-Frost Bridge Rd, 8 Sep 2002, *S.W. Leonard 10903* (MMNS). **Tennessee**. McNairy Co.: 1.5 mi W of New Hope, 16 Aug 1958, H. DeSelm 1898 (TENN) [also collected here in recent years by D. Estes for APSC, and cultivated by the senior author; see notes above].

The following two disjunct western collections are close to *Rudbeckia terranigrae* but their inclusion remains uncertain. The collection from Texas may represent another undescribed taxon.

(1) **Missouri**. Greene Co.: Springfield, along Fremont St just S of intersection with Seminole, open lot, 2 Oct 1973, *P. Nelson 111* (MUHW ex SMS). Initial identification was *R. triloba*. The collection at MUHW lacks lower leaves and had been cut early in the year, but it appears to match *R. terranigrae* well, with a tight cluster of blackish mid-cauline leaves and six heads arrayed more or less in plane. Yet without any further records of similar plants from Missouri, it is possible that this urban collection just represents a waif or has a cultivated origin.

(2) **Texas**. Gillespie Co.: Fredericksburg, Oct 1850, *G. Thurber 71* (GH "Syn. Fl. N. Amer."; NY). This collection lacks lower stem and lower leaves, and does not indicate habitat. The plant is unusually robust, with relatively long internodes; phyllaries are ca. 4–5 mm wide; and rays are up to ca. 20–30 mm long. Blackland soils similar to the Black Belt further east are extensive in central Texas but do not generally occur on the Edwards Plateau, where Fredericksburg is located (Diggs et al. 1999; Peacock & Schauwecker 2003; Echols & Zomlefer 2010). The only member of the *fulgida* complex reported from Texas in recent treatments is var. *palustris* (Correll & Johnson 1970; Urbatsch & Cox

2006). The description of var. *palustris* by Correll and Johnson noted that it is "stoloniferous... [with] most of the leafy tufts arising at the ends of the stolons"; and "rare in moist places w. to Edwards Plateau..." It is likely that they included plants like the Thurber collection in their circumscription.

Rudbeckia terranigrae is similar to the more northern species, *R. tenax* and *R. speciosa*, but there is little or no overlap in ranges and plants with intermediate morphology are unknown. It also resembles typical *R. fulgida* of more acid soils in southeastern states, which is virtually absent on the Gulf Coastal Plain. The most eastern record of *R. terranigrae* is from Barbour Co., Alabama, on the southeast side of the Black Belt, where the Demopolis Chalk is replaced by the Cuseeta Sand member of the Ripley Formation. Further east there are local blackland soils on the Coastal Plain of Georgia, where plants identified as *R. fulgida* need further study to determine if there is intergradation. A collection from Houston Co., Georgia (*L.E. Echols 414*, GA), does suggest *R. terranigrae* in its clustered mid-stem leaves, but the overall weight of its characters indicates *R. fulgida*.

Further research is needed to compare *Rudbeckia terranigrae* with the following similar collections from cedar glades and associated remnants of historical "barrens" in central Tennessee and elsewhere (Fig. 4). Some of these collections appear to represent another undescribed taxon: "*R. augusta*" ined. Others may be transitional to *R. tenax* or to *R. fulgida*. Those from Ohio might be interpreted as transitional from *R. tenax* to *R. sullivantii*. Question marks show uncertain assignment; brackets contain senior author's notes.

Alabama. Colbert Co.: Rosebud Barren, 21 Aug 1992, *H.R. DeSelm s.n.* (TENN). Franklin Co.: 1.5 air-miles N of White Oak along Co. Rd. 83, 0.6 mi E of jct. with St. Rd. 247, 21 Aug 2011, *B.R. Keener 6633* (UWAL). Decatur Co., 1878, *G.R. Vasey s.n.* (US). **?Georgia**. Dade Co.: large colony in center of overgrown pasture, along US Rt. 11, 6.1 mi N of post office at Rising Fawn, 24 Aug 1952, *R.E. Perdue 1365* (US). Richmond Co.: Augusta, flat pine barrens, 10 Oct 1898, *A. Cuthbert Herb No. 323* (NY) [incomplete and perhaps mixed collection, suggesting transition from *terranigrae* to *fulgida*]. Houston Co.: recent collections of *L. Echols* to be accessed and studied further (UGA). **Kentucky**. Edmonson Co.: Mammoth Cave, 7 Sep 1940, *E.L. Braun 3567* (US); Mammoth Cave National Park, river flat opening in beech-maple woods, 14 Aug 1948, *H. Lix 467* (US). ?Grayson Co.: abundant in roadside ditch N of Holly (near Leitchfield), 22 Aug 1953, *H.E. Ahles 7572* (NY) [may tend towards *deamii*]. **Ohio**. Adams Co.: SW corner Oliver Township, openings in post oak area, mesic woods, 11 Aug 1954/56, *E.L. Braun s.n.* (OS); Co. Franklin Twp., Jaybird Quad., along unnamed tributary of Scioto Brush Creek, SW., St. Rt. 32 bridge, 0.7 mi SW. of St. Rt. 73. 18 Aug 1982, *A.W. Cusick 21969* (NY) [less hairy than *Braun* coll.]. Belmont Co.: N of jct. St Rte 148 & Co Rte 92, Wayne Twp., frequent, S-facing slope, limestone rubble, 22 Sep 1982 *A.W. Cusick 22186* (OS); [same location] 15 Aug 1983, *A.W. Cusick 22866* (NY). Franklin Co.: Georgesville, 29 Aug 1892, *W.A. Kellerman s.n.* (OS). Highland Co.: wooded bottomlands near var. *umbrosa* but without apparent intergradation, 12 Aug 1945, *A. Cronquist s.n.* (NY). Lawrence Co.: Dean Forest, 10 Aug 1941, *L.L. Pontius, F. Bartley & E.L. Crist s.n.* (OS). Marion Co.: section 23, roadside prairie remnant, 28 Aug 1952, *H.R.DeSelm s.n.* (OS). ?Pickaway Co.: Cedar Bluff along Darby Creek, 5 Aug 1959, *F. Bartley 2387 & 2400* (NY, OS). Shelby Co.: Loramie Reservoir, 24 Aug 1897, *W.A. Kellerman & A.R. Beatty s.n.* (OS). Union Co.: Darby Township, 20 Aug 1897, *W.A. Kellerman s.n.* (OS). **?South Carolina**. Edgefield Co.: [data missing] (US) [unusually robust plant with 17 heads]. **Tennessee**. Franklin Co.: in cultivation at Lexington, Kentucky, but originally collected from along Buncombe Road ca. 1 air-miles SE of Belvedere, near junction with gravel road at top of hill, 23 Sep 2013, *J.J.N. Campbell s.n.* (APSC). Marion Co.: W-facing midslope cedar barren just N of Gray's Point with *Liatris aspera*, *Ruellia* sp., *Scutellaria leonardii*, [fall] 2004, *J. Beck 6260* (TENN). Overton Co.: dolomitic ledges by Tenn 84 4.7 mi N of Monterey, 13 Aug 1970, *R. Kral 40502* (GA, UNA). Rutherford Co.: Lavergne, 18 Aug 1897, *H. Eggert s.n.* (MO); stream in glade 7 mi E of Murfreesboro, 16 Aug 1958, *H.R. DeSelm 1912* (TENN). ?Williamson Co.: Haffner Woods on Owl Hollow Road about 1.8 mi W of Rte 102, 30 Aug 1994, *H.R. DeSelm s.n.* (TENN) [incomplete coll.]. Wilson Co.: barren N of Vesta, 2 Aug 1988, *H.R. DeSelm s.n.* (TENN).

In addition, J. Campbell and D. Estes (pers. comm.) have collections of such plants from some of the same counties in Tennessee, to be accessioned at APSC. They occur within 100 meters of *R. tenax* at some sites, but plants with intermediate morphology are unknown. They usually occur on deeper or damper soil, and the flowering peak is usually 2–3 weeks later than *R. tenax* (see key below).

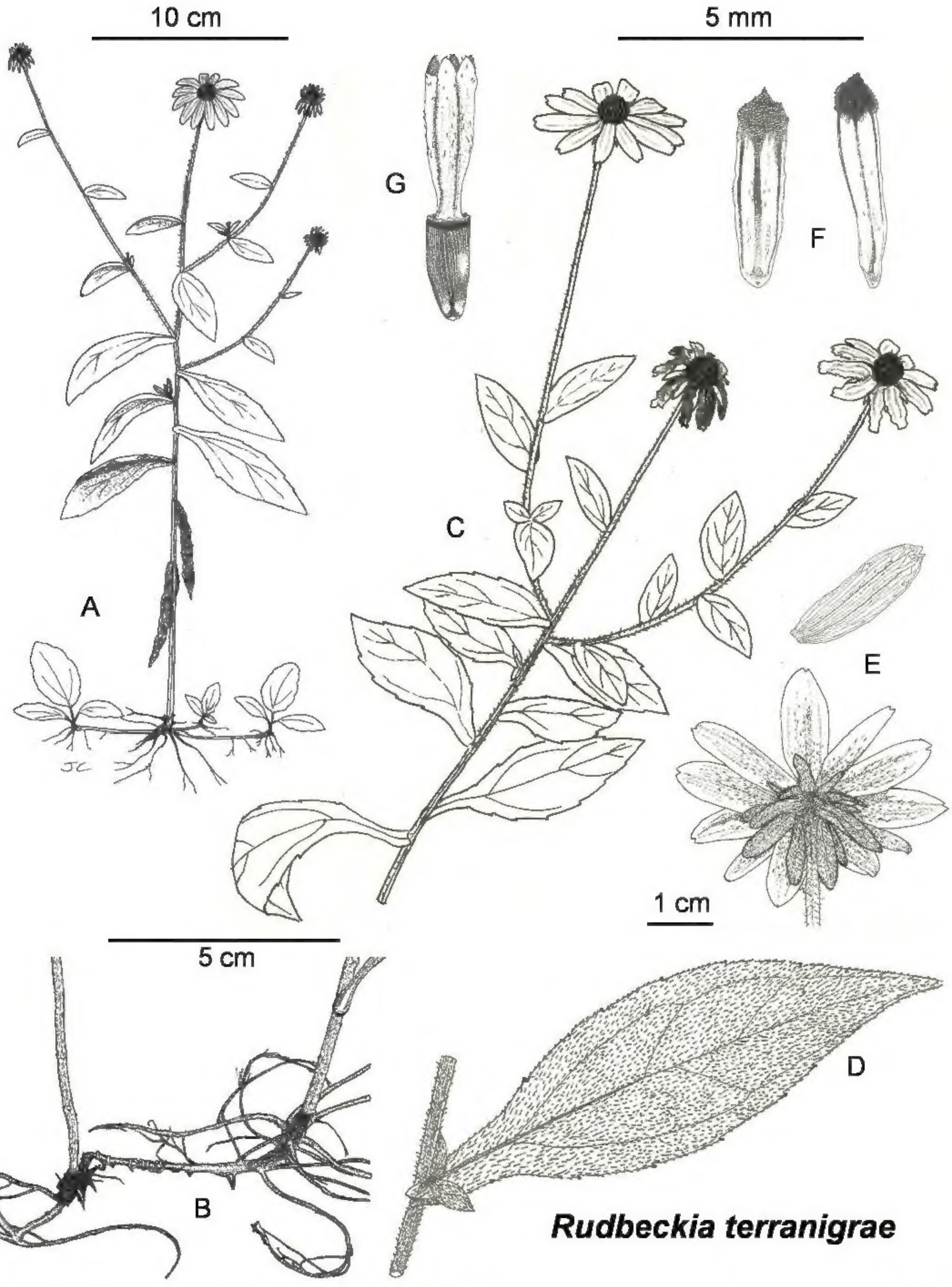

Figure 2. Line-drawings of *Rudbeckia terranigrae*, all based on type material from Chickasaw Co., Mississippi. A: whole plant early in flowering season. B: stem bases and stolons. C: upper portion of flowering shoot (later than A). D: mid-cauline leaf. E: flowering head from below, and ray petal. F: receptacular bracts, outer (center) and inner (right). G: disc floret. [By RS except A.]

Figure 3 [this page and next two]. Photographs of *Rudbeckia terranigrae*, all except E from the Pulliam Prairie in August 2009 (Chickasaw County, Mississippi).

A. Plants in foreground at base of prairie with much *Silphium*, just above wooded riparian zone.
B. Large branched plant seen from above. C: head seen from below.
D. Weak reclining plant at edge of dried stream within thin riparian woods, seen from above.
E. Cultivated plant before flowering in June 2010, with distinctive cluster of mid-cauline leaves.

A

B

C

D

E

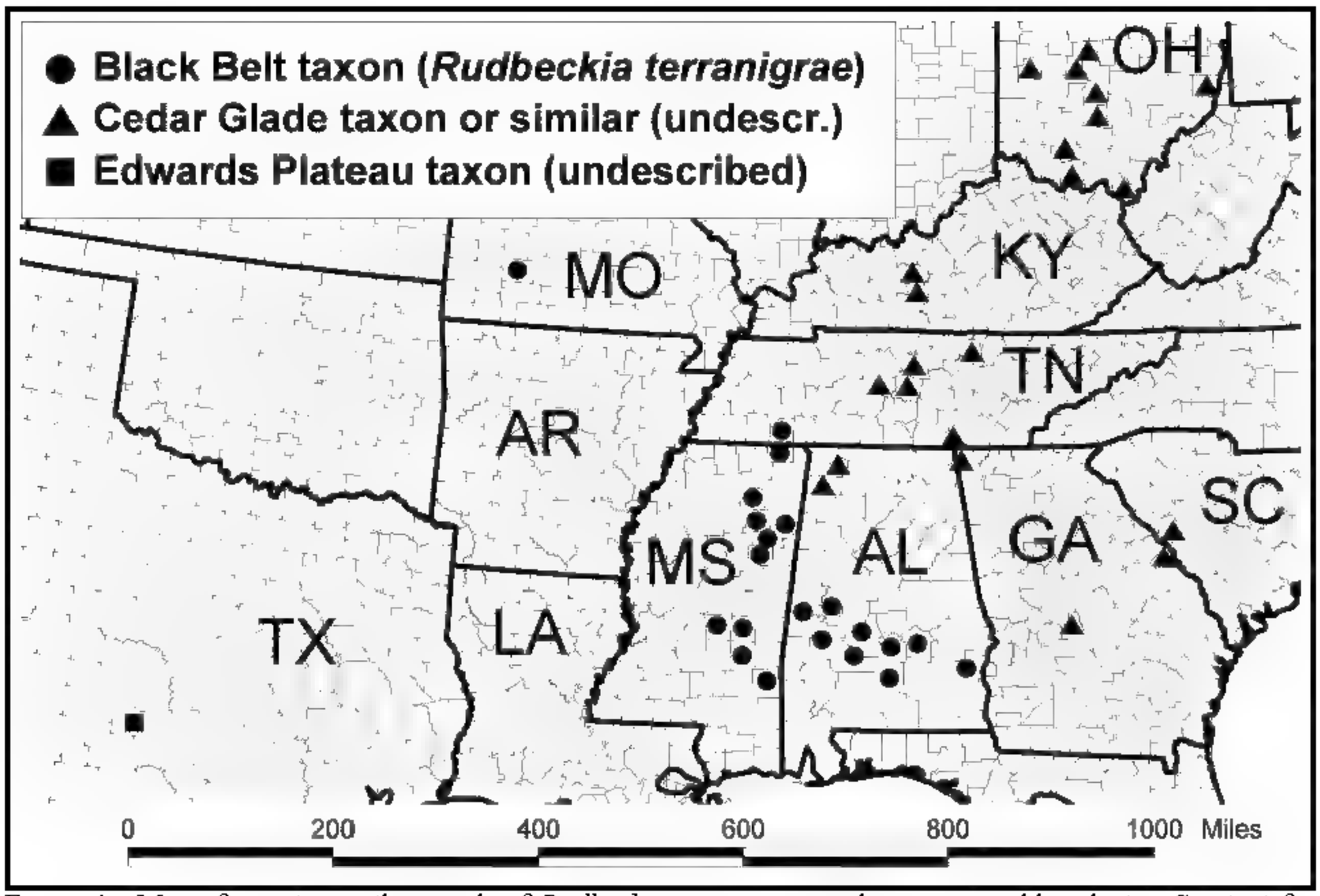

Figure 4 Map of counties with records of *Rudbeckia terranigrae* and *terranigrae*-like plants See text for explanation of taxa and sources of data, the Missouri record remains tentative

PROVISIONAL KEY TO TAXA OF THE *RUDBECKIA FULGIDA* COMPLEX

The following synoptic key summarizes an attempt to define and identify the taxa, based on a range of characters, and to organize them in a hypothetical phylogeny Within couplets, the order of taxa is generally set out from relatively southern taxa to more northern taxa and towards taxa with higher reported chromosome numbers, distinct stolons, and relatively broad lower leaves "L/W" length width ratio

Development of this key was initially based on Small (1933) and Fernald (1950), who recognized several of the taxa treated here But it became modified by much experience in the field and herbaria, especially at the Gray Herbarium, where much early annotation by Asa Gray and his contemporaries is available, and at the New York Botanical Garden, where material of John Kunkel Small, Charles Lawrence Boynton, and Chauncy Delos Beadle is available, including several types All of the taxa keyed out below have been combined within *Rudbeckia fulgida* by one or more of the major post-Fernald (1950) treatments, although some have been treated as varieties (Perdue 1957, Cronquist 1980, Gleason & Cronquist 1991, Urbatsh & Cox 2006)

Further testing and adjustment of the key is desirable before it can be considered reliable for practical purposes Many collections lack plant bases with lower leaves and stolons, making some couplets difficult to apply The 'stolons' are relatively short, determinate, rooting offsets, each terminating in a leafy tuft that can become the base of a flowering stem during the subsequent year In most taxa, leaves vary considerably from base to summit of plants The basal tufts of leaves, formed on offsets in summer to spring, usually have broader shape than most cauline leaves The lowest cauline leaves usually resemble basal leaves in blade shape but tend to be larger and have

more distinct petioles, which are particularly long in some taxa. Middle cauline leaves tend to be smaller than lower leaves in most taxa, and usually have less distinct petioles that are broadly winged. Upper cauline leaves are progressively smaller, with little or no distinct petiolar bases.

The presence or absence of cilia on the summits of the paleae (receptacular bracts of disc florets, also known as 'pales' or 'chaff') has been emphasized by Small and Fernald in their primary divisions of taxa. However, this character remains difficult to determine in many collections. It is variable within some taxa, even within an inflorescence or head, as is the apical shape of paleae. Better description and definition of terms is still needed. In some collections, lines of cells appear wadded together in pale waxy summits, as opposed to forming individually distinct hairs. Do such collections reflect a stage in development, or do they represent an intermediate genetic condition?

1. Basal and lower cauline leaves without distinct petioles, not much different from mid-cauline leaves, narrowly lanceolate to linear, usually 1–3 cm wide, entire to remotely and shallowly dentate; paleae glabrous or nearly so (sometimes with sparse hairs on outer base), entire or slightly erose, marginal veins glossy-blackish and often sharply distinct; offsets from caudex usually not spreading more than 1 cm (rarely 2–3 cm); plants generally with ascending leaves and branches [*truncata-missouriensis* subgroup, typical of xeric calcareous sites on south-facing hillsides and clifftops]

   2. Plants glabrous or nearly so, except for ciliate leaf margins, sometimes thinly hirsute midribs and stems; lower leaves mostly (1–)1.5–3(–5) cm wide, elliptic to narrowly lanceolate, dentate to entire; flowering branches mostly spreading; paleae usually greenish to brownish or darker, grading into blackish veins (the midrib less distinct than marginal veins); rays mostly 8–20 mm long ..... **Rudbeckia truncata**

   2. Plants densely villous-hirsute (except for paleae); lower leaves mostly (0.5–)1–1.5(–2) cm wide, linear-lanceolate, entire; flowering branches mostly ascending; paleae usually pale whitish green with sharply contrasting blackish veins (the midrib often as distinct as marginal veins); rays mostly 15–25 mm long ..... **Rudbeckia missouriensis**

1. Basal and lower cauline leaves with distinct petioles and broader shape than mid-cauline leaves, lanceolate to ovate, usually 1–10 cm wide, almost entire to sharply dentate; paleae usually with at least a few hairs on outer surface, often irregularly erose-ciliate on sides, usually with marginal veins brownish to blackish and not sharply distinct; offsets from caudex short (0–3 cm), or distinct (substoloniferous) and spreading (3–)5–12(–15) cm from stem bases after initial flowering; plants generally with spreading leaves and branches

   3. Largest basal and lower cauline leaves with petioles usually 2–12 cm long (to 15 cm in cultivation), blades cuneate, 2–8(–10) × 1–5(–7) cm; mid-cauline leaves shallowly dentate to almost entire, the regular teeth usually no more than 1(–2) mm deep (excepting occasional irregular lacerations); paleae often with a few hairs on inner surfaces, the outer ones often with distinctly thickened waxy apices; rays ca. 6–14, mostly (0.5–)1–2.5(–3) cm long [*fulgida-tenax* subgroup, typical of submesic to subxeric sites on varied substrates]

      4. Paleae, at least the outer ones, with distinct cilia (ca. 0.1–0.3 mm long) uniformly arrayed over relatively thin apices without erose or waxy interruptions, without any hairs on inner surface; discs of primary heads averaging ca. 8–12 mm wide; plants without distinct basal offsets exceeding 1–2(–3) cm long; leaves up to 2–3(–4) cm wide, usually plain green (somewhat yellowish when dried), without pronounced waxy thickening, the teeth often

thickened but not much inrolled [*R. fulgida*, sensu stricto, plants generally typical of non-calcareous soils]

5. Basal and lowest cauline leaves mostly 1–2 cm wide; mid-cauline leaves mostly 3–5(–9) × 0.5–1 cm, lanceolate to oblanceolate or spathulate, tapering to a broadly winged indistinct petiole or sessile; involucres usually 5–9 mm long, the larger phyllaries 1–2 mm wide; discs mostly 0.8–1.2 cm wide, rays mostly 1–1.5 cm long ..... **Rudbeckia fulgida var. spathulata**

5. Basal and lowest cauline leaves mostly 2–3 cm wide; mid-cauline leaves mostly 5–15(–20) × 1–2 cm, lanceolate, tapering to a distinct petiole; involucres usually 10–22 mm long, the larger phyllaries 2.5–7 mm wide; discs mostly 1–1.5 cm wide, rays mostly 1.5–2 cm long ..... **Rudbeckia fulgida var. fulgida**

4. Paleae eciliate or (especially outer ones) irregularly erose to thinly ciliate, the hairs interrupted by a waxy-thickened apical point, the inner surface usually with a few hairs; discs of primary heads (not later ones) averaging ca. 12–16 mm wide; plants with distinct stoloniferous offsets (2–)3–10 cm long; leaves up to 3–5(–7) cm wide, plain to bluish-green (especially when dried), usually with pronounced waxy thickening (often minutely reticulate or pebbly below) and slightly revolute, including margins between the teeth, which are usually inrolled [plants generally typical of calcareous soils]

6. Heads opening more or less together in (June) mid-July to mid-August (September), (1–)2–7(–12+ in cultivation), mostly 20–60 cm above lowest node of inflorescence on long bracteate peduncles; mid-cauline leaves mostly 0.5–2.5 cm wide, with L/W 4–10, tapering to less distinct petiolar bases 2–4(–8) mm wide; stems and leaves thinly to densely pilose with mostly appressed soft hairs, usually plain green

7. Mid-stem leaves mostly with L/W ca. 4–6 (ca. 5–10 × 1–2.5 cm), and with 3–5(–8) distinct leaf teeth on each margin, their sinuses no more than ca. 1 mm deep; petioles of basal leaves mostly 3–6 cm; rays mostly 1–2 cm long ..... **Rudbeckia tenax**

7. Mid-stem leaves mostly with L/W ca. 7–12 (ca. 10–15 × 0.7–1.5 cm), and with 1–3(–5) distinct teeth on each margin, irregularly spaced and coarse, their sinuses generally 1–10 mm deep; petioles of basal leaves mostly 6–12 cm; rays mostly 1.5–2.5 cm ..... **Rudbeckia speciosa, sensu stricto**

6. Heads opening in (July) early August to mid-September (October), often solitary or with one distinctly larger, mostly 10–40 cm above lowest node of inflorescence on long or short bracteate peduncles; mid-cauline leaves mostly 1.5–4.5 cm wide, with L/W 3–6, their distinct petiolar bases 4–8(–14) mm wide with almost parallel sides; stems and leaves thinly to densely rough-hirsute with mostly spreading pustulate hairs, yellowish- to deep bluish-green

8. Larger mid-stem leaves usually ascending and forming an overlapping cluster [especially when pressed] of 6–12 along 10–15 cm of stem [with flowering often delayed during drought], mostly 6–17 × 2–4.5 cm; leaves pale yellowish-green or often bluish-black when dried; heads usually solitary at first in (July–) early to mid-August, but often adding 2–5+ (–12+ especially in cultivation) until mid-September (–October) ..... **Rudbeckia terranigrae**

8. Larger mid-stem leaves ascending to spreading [prone to wilt during drought as in *tenax*], not forming a pronounced cluster along the stem, mostly 4–9 × 1.5–3.5 cm; leaves usually deep glossy green; heads 1–5 (–12+ in cultivation), opening more or less together in (July–) early to mid-August (–September) ..... **Rudbeckia "augusta" ined.**

3. Largest basal and lower cauline leaves with (8–)12–30(–40) cm petioles, their blades broadly cuneate, truncate or subcordate, (4–)8–15(–20) × (2–)3–10(–12) cm; mid-cauline leaves often coarsely dentate with teeth at least 2 mm deep; paleae usually glabrous on inner surfaces (or with 1-3 hairs), the outer ones usually without thickened waxy apices; rays ca. 12–21, mostly (1)1.5–3(–4) cm long [*umbrosa-palustris* subgroup, typical of submesic to subhydric sites on more or less base-rich soils but often mixed with sand]

9. Plants without stolons, the basal offsets at most 1 cm long, often not producing new tufts of leaves until spring; largest leaves basal to middle cauline, subcordate, broadly ovate (L/W ca. 1–1.5), their petioles usually <20 cm long, their margins dentate with elongated calluses 0.3–1 mm high (L/W ca. 2–2.5) and usually without pronounced waxy thickening; leaves in inflorescence sometimes subopposite to opposite; paleae with distinct (0.1–)0.2–0.3(–0.4) mm cilia uniformly arrayed over relatively thin apices without erose or waxy interruptions; discs averaging ca. 1 cm wide, rays mostly 1–2 cm long ..... **Rudbeckia umbrosa**

9. Plants usually with distinct stolons 1–10 cm long, producing new tufts of leaves during summer to fall; largest leaves basal to lowest cauline, cuneate, truncate or subcordate, broadly ovate to lanceolate (L/W ca. 1–4), their petioles often 20–30(–40) cm long, their margins usually shallow crenate-dentate with domed calluses 0.3–0.5 mm high (L/W ca. 1–1.5) and pronounced waxy thickening; leaves in inflorescence clearly alternate; paleae eciliate or with 0.1–0.2(–0.3) mm cilia thinly arrayed over the apex, often with erose or waxy interruptions (variable within most taxa); discs averaging 1–1.5 cm wide, rays mostly (1–)1.5–3(–4) cm long

10. Largest basal leaf blades with L/W mostly 1.5–4, cuneate to truncate; leaves yellowish- or bluish-green (when dried), relatively thin, glabrate to hirsute-hispid, the cauline ones subentire to serrate (teeth projecting mostly < 2 mm); basal stoloniferous offsets usually <5 cm long; rays mostly 1–2.5(–3) cm long; paleae usually somewhat ciliate on sides and apex, or just erose at apex

11. Basal leaf blades ovate (L/W ca. 1.5–2), cuneate, the petiole broadly winged in distal 20–30%; plants usually drying to bluish-green, hirsute to hispid; stems usually ca. 3 mm thick at middle [discs averaging ca. 1.5 cm wide; rays mostly 15–25 × 3–5 mm] ..... **Rudbeckia aff. palustris; "speciosa" auctores B**

11. Basal leaf blades broadly to narrowly lanceolate (L/W ca. 2–4), cuneate to truncate (or subcordate in unusually robust plants), the petiole in broad-leaved plants usually not winged except in distal 10–20%; plants usually drying to yellowish-green, glabrate to thinly hirsute; stems usually ca. 2 mm thick at middle (but up to 6 mm in cultivation)

12. Basal leaves broadly lanceolate (L/W ca. 2–3), cuneate to truncate (or subcordate); discs averaging ca. 9–12 mm wide; rays mostly 10–20 × 2.5–4 mm; paleae distinctly ciliate ..... **Rudbeckia palustris, sensu stricto**

12. Basal leaves narrowly lanceolate (L W ca. 3 4), cuneate; discs averaging ca. 12 16 mm wide; rays mostly 15 25 × 3 5 mm; paleae thinly ciliate to erose ..... **Rudbeckia aff. palustris; "speciosa" auctores C**

10. Largest basal leaf blades with L W mostly 1 2, truncate to subcordate; leaves usually dark bluish-green (especially when dried), relatively thick, coarsely hirsute-hispid, the cauline ones crenate to dentate (teeth often projecting 3 4 mm); basal stoloniferous offsets usually 5 10 cm long; rays mostly (1.5)2 3(4) cm long; paleae ciliate to eciliate

13. Plants not distinctly grayish-hairy, the stems with sparse to dense stiff, antrorse or retrorse hairs (mostly 0.5 1 mm), up to ca. 0.3 0.8 m tall; larger basal leaves usually with ca. 15 20 cm petioles, broadly cuneate, truncate or subcordate, 4–9 cm wide, subentire to crenate; leaves reduced in width up the stem, lanceolate to ovate to subrhombic, usually without subamplexicaul bases or long acuminate apices, crenate to dentate; rays mostly 2 3 cm long; paleae stramineous to orange-brownish, with or without blackening of midrib

14. Larger cauline leaves crenate-dentate with teeth projecting 1 2(3) mm from sinuses; largest basal leaves up to 6(9) cm wide, with L W ca. 1.5 2; middle to upper cauline leaves ovate-lanceolate (widest about a third from base); rays ca. (15)20(25) × 4–6 mm; paleae densely to thinly ciliate ..... **Rudbeckia chapmanii** and allies; including **"speciosa" auctores D**

14. Larger cauline leaves sharply dentate with teeth projecting (1)2 5 mm from sinuses; largest basal leaves up to 9(12) cm wide, with L W ca. 1 1.5; middle to upper cauline leaves ovate-lanceolate to subrhombic (often widest just below middle); rays ca. (20)30(35) × 5 9 mm; paleae thinly ciliate to eciliate ..... **Rudbeckia sullivantii**

13. Plants grayish-hairy, the stems with dense fine retrorse hairs (mostly 1 2 mm), up to ca. 0.6 1 m tall; larger basal leaves usually with ca. 10 15 cm petioles, broadly cuneate or occasionally subtruncate, 3 6 cm wide, crenate to shallowly dentate; leaves about as wide at mid-stem as most basal leaves, mostly ovate-lanceolate in central third of blade but often with broad subamplexicaul petiolar bases and long-acuminate apices, shallowly to irregularly dentate; rays mostly 1.5 2.5 cm long; paleae whitish green to stramineous, usually with little blackening of midrib ..... **Rudbeckia deamii**

NOTES ON TAXA

The sequence of taxa below follows the synoptic key above. For each of these taxa, series of representative images are being assembled at the senior author's website (Campbell 2013). Chromosome numbers come from cited literature plus provisional estimates from flow cytometry (J. Campbell, P. Zale, et al., in prep.). Much further determination of numbers is desirable given the reported variation. Ranges and habitats provided below are based primarily on specimens annotated by the senior author at several herbaria (APSC, BHO, EKY, GA, GH, KY, IBE, MISS, MISSA, MMNS, MO, MU, MUHW, NCU, NY, OS, TENN, UNA, US, USCH, WVA). Uncertain data are indicated below by "?"; these come from specimens with only tentative identification here, or with unverified information from other sources (as cited below).

TRUNCATA-MISSOURIENSIS SUBGROUP

***Rudbeckia truncata* Small**

2n: ?38 (Georgia) and ?57 (Kentucky); estimates from Campbell et al. (in prep.).

Range: southern Ridge & Valley and western edge of Cumberland Plateau; Georgia (Catoosa & Floyd Cos.), ?Alabama (Small 1933), Tennessee (Claiborne, Union, Hawkins, Greene & Hamblen Cos.; A. Floden, pers. comm.) and Kentucky (McCreary, Pulaski, Wayne & Jessamine Cos.).

Habitat: xeric calcareous clifftops, ledges and rocky glades, sometimes thin woods with red cedars.

Notes. Small (1933) treated this taxon as a species, along with other segregates of *Rudbeckia fulgida*, and his circumscription is largely accepted here but extended to include plants further north. *Rudbeckia truncata* is distinct in its dense clumps, long narrow basal leaves, narrow truncate cauline leaves, and eciliate bracts of disc florets. The type of *R. truncata* (NY) is a collection of J.K. Small: 6 12 Aug 1895, along the Chickamauga Creek near Ringgold, Catoosa Co., Georgia. Small (1898) stated that *R. truncata* occurs "In meadows and dry soils, northwestern Georgia... quite common in the limestone districts... There is a specimen almost identical with mine in the herbarium of Columbia University [Chapman Herbarium], collected many years ago at Rome, Georgia" [now at NY and US]. Elsewhere in Georgia, *R. truncata* has been recently discovered by J. Campbell and M. Medley in the Coosa Grand Prairie of Floyd Co. The collection of E.L. Braun's from Cox Bend, Pulaski Co., Kentucky (*Braun 2630*, 8 Sep 1939, NY), was annotated by Cronquist as "correctly identified with *R. truncata* but no more than a variety, at best, of *R. fulgida*." There appears to be considerable variation between these disjunct populations. The apparent triploids in Kentucky are mostly less hairy than the diploid in Georgia, but the Jessamine Co. plants (on overlook facing Pollys Bend west of US 27) are hairier than the others and have suggested a transition to *R. missouriensis*.

***Rudbeckia missouriensis* Engelm. ex C.L. Boynt. & Beadle**

Rudbeckia fulgida var. *missouriensis* (Engelm.) Cronq.

2n: 38 (Vahidy et al. 1987; Palmer et al. 2009; Campbell et al., in prep.)

Range: West Gulf Coastal Plain (Pleistocene to Miocene sections west of Mississippi Rv.), Ouachita Mountains, Ozark Mountains and nearby hills; Texas, Louisiana, Oklahoma, Arkansas, Missouri, Illinois.

Habitat: on Coastal Plain, prairie patches on calcareous clays, generally well-drained but often with a high shrink-swell potential and slow permeability (Brown et al. 2002; Allen et al. 2004); in Oucachita Mountains, generally uncommon, xeric glades along more base-rich bluffs; in Ozarks, "glades, ledges and tops of bluffs, rock outcrops in upland prairies and rocky openings of dry upland forests, rarely banks of streams, also roadsides, usually on limestone and dolomite substrates" (Yatskievych 2006).

Notes. The distinction of *Rudbeckia missouriensis* from *R. fulgida* was initially doubted by some eastern botanists (Meehan 1896). Although locally abundant within its main range, the species is not verified east of the Mississippi River except in southern Illinois. It appears to differ from the more eastern *R. truncata* mostly in its denser pubescence and narrower leaves. Plants of either taxon should be searched for within intervening regions. *Rudbeckia missouriensis* has been reported from Kentucky but no convincing collections have been seen (Medley 1993); see note under *R. truncata*.

FULGIDA-TENAX SUBGROUP

***Rudbeckia fulgida* Ait var. *spathulata* (Michx.) Perdue**

Rudbeckia spathulata Michx.

? *Rudbeckia foliosa* C.L. Boynt. & Beadle. This name has been applied to plants from Louisiana to North Carolina "mostly of marly places" (Small 1903). They appear to differ from some var. *spathulata* in the relatively broad shape of their leaves; they may be transitional to var. *fulgida*.

2n: ?38 (McCrea 1981; Campbell et al., in prep.).

Range: largely restricted to the coastal plains of southeastern states, but much less widespread on the Gulf Coastal Plain; ?Texas, Mississippi, Alabama, Tennessee (rare), ?Kentucky (rare if at all); Georgia, Louisiana, South Carolina, North Carolina (core of range underlined); West Virginia (rare), Virginia, D.C., ?Maryland, Delaware.

Habitat: varied types of opening or thin woods, often with pines or scrubby oaks; "low woods, meadows and clearings" (Fernald 1950). Labels on collections indicate seasonally damp soils (ditches, flats, swales, floodplains) with sandy, clayey, or calcareous character, from pitcher plant savannahs to rocky glades.

Notes. Several collections appear transitional to var. *fulgida*, especially in the north. As outlined here, var. *spathulata* may be just be a miscellany of intergrading depauperate forms with leaves reduced in width (more lanceolate) or length (more spathulate); more analytical work is needed. A few collections included here from Louisiana, Georgia, Mississippi and South Carolina have leaves that are densely scabrous-hirsute and exceptionally narrow, ca. 3 6 mm wide, and linear-lanceolate to oblong, not spathulate; these plants might represent another distinct variety.

Rudbeckia fulgida* Ait. var. *fulgida

? *Rudbeckia acuminata* C.L. Boynt. & Beadle, based on types at NY and US, ex. Biltmore Herbarium 14723b, 20 Aug 1903, from "Rocky slopes near Harriman, Tennessee" [Roane Co.]. This collection from e. Tennessee (and a similar one from Knox Co. at US) may just represent a robust form of typical *R. fulgida*, but it has suggested a distinct variant or transition to other taxa (such as *R. tenax* or *R. umbrosa*). It has unusually broad, darker leaves up to 3 4 cm wide.

2n: ?38 (in southern populations; McCrea 1981) or 76 (McCrea 1981, Palmer et al. 2009)

Range: mostly in or near southern Appalachian regions, Piedmont and mid-Atlantic Coastal Plain; Alabama; Georgia*, Louisiana*, South Carolina*, North Carolina*, Virginia*, West Virginia (core of range underlined); D.C., Maryland, Delaware, New Jersey, Pennsylvania; local to uncommon in Tennessee, Kentucky and Ohio. Several collections from some states (*) appear transitional to var. *spathulata*. Both varieties have been distributed by some nurseries for ornamental use (S. Stieve, pers. comm.), but var. *fulgida* has been used much more widely, with early introduction to Europe (Dillenius 1732).

Habitat: open to slightly shaded areas, often disturbed such as along roads, but avoiding xeric or hydric extremes; "dry or moist, open or shaded places" (Fernald 1950); notes on collections indicate that plants typically occur on somewhat acid soils and are rare on distinctly calcareous soils.

Notes. The name *Rudbeckia fulgida* has been widely applied to most of the taxa treated in this paper, allowing much confusion in published ranges and habitats. Despite many reports, typical *R. fulgida* is unknown in mid-western regions, where most records probably refer to *R. speciosa*. Further south and east, there is also confusion due to apparent intergradation with *R. tenax*, especially along roads in the Cumberland Plateau and Ridge & Valley of Alabama, Georgia, Tennessee, Kentucky and Ohio; see notes under *R. tenax*.

***Rudbeckia tenax* C.L. Boynt. & Beadle**

Rudbeckia fulgida var. *fulgida*, in part, of Perdue (1957), Kral (1975) and most recent authors.

2n: ?38 and ?76; possibly also 95 and 114 (Campbell et al., in prep.).

Range: Interior Low Plateaus (mostly), southern Cumberland Plateau, southern Ridge & Valley, and locally on central Gulf Coastal Plain; ?Illinois, Indiana, Ohio; Alabama, Georgia, Tennessee, Kentucky (core of range underlined); Mississippi, Florida.

Habitat: xeric to xerohydric calcareous glades, thin woods and roadsides, often with red cedars; "dry woods and clearings" (Fernald 1950). *Rudbeckia tenax* prospers along infrequently mowed gravelly roadsides, and it appears to have spread locally onto originally non-calcareous soils where disturbance such as road-building with gravel, and perhaps burning, may have enriched the soil. Such

trends are suggested partly from observations of the senior author and D. Estes (pers. comm.) at Catoosa Wildlife Management Area in Morgan Co., Tennessee.

Notes. This variable species was recognized by Small (1933) and Fernald (1950) but it has been largely overlooked for 50 years. The frequent lack of plant bases in collections has contributed to confusion with other taxa. The stoloniferous habit and largely eciliate paleae of *Rudbeckia tenax*, illustrated well as "*R. fulgida*" by Kral (1975), generally distinguish the species from true *R. fulgida*. However, there appears to be some intergradation, especially in the Appalachian Plateaus and Ridge and Valley. Both taxa can become locally weedy on roadsides or similarly disturbed sites, and possible hybrids have been recorded from such sites where ranges overlap. There has also been confusion with *R. speciosa*. Some plants of typical *R. speciosa* resemble *R. tenax*, especially in ne. Kentucky, se. Indiana, and se. Ohio, and these have mistakenly been called "*tenax-speciosa* intermediates" by the senior author. Some relatively robust plants suggest transitions to species in the *umbrosa-palustris* subgroup.

***Rudbeckia speciosa* Wenderoth sensu stricto; "*speciosa* A"**

2n: 76 (McCrea 1981; Urbatsch et al. 2000; Palmer et al. 2009; Campbell et al., in prep.)

Range: mostly on Glacial Till Plains and extending along valleys into western Appalachian regions, including parts of the Allegheny Plateau and northern Ridge & Valley, perhaps also on the mid-Atlantic Coastal Plain; widely distributed but apparently local to rare as a native plant within most of its range: Missouri, Illinois, Wisconsin; n. Kentucky, Indiana, Michigan, Ohio, Pennsylvania (core of range underlined); ne. Tennessee, w. Virginia [2500 ft a.s.l.], West Virginia [1550 ft a.s.l.], se. New York, Connecticut, ?Massachusetts, s. Ontario, ?s. Quebec. [An 1870s collection from Ontario is at NY: "*J. Macoun No. 9*. Shore of Lake Huron. What is this? Can it be a *Rudbeckia*?"] Some records are probably from horticultural escapes, especially in eastern regions.

Habitat: on generally base-rich soils (calcareous or dolomitic); "woods and bottomlands, local" (Fernald 1950). It may be most common in thin woods and meadows on seeps or swales with a tendency to hydrological variation, while *Rudbeckia tenax* (or *R. missouriensis*) tends to be on more consistently xeric rocky sites, and *R. sullivantii* (or *R. palustris*) tends to be on more damp to marshy soils. More data are needed to compare habitats of these taxa in regions where they overlap.

Notes. These rather variable plants can easily be confused with *Rudbeckia tenax* if whole plants are not collected. Compared to *R. tenax*, they have unusually elongated, irregularly dentate or lacerate cauline leaves and often relatively large basal leaves. Some largely sterile plants of this species have become widely propagated as ornamentals across eastern North America and Europe during the past two centuries. These plants were often named *R. fulgida* (Meehan 1896) and they appear to include the plant illustrated as "*R. fulgida*" by Meehan (1879-80). A cultivar informally named "*Rudbeckia neumanii*" was distributed over a century ago, and a plant named "Viette's Little Suzy" was more recently distributed from nurseries in Ohio (S. Stieve, pers. comm.). The name "*R. speciosa*" has been widely misapplied to other taxa in the past (including previous notes and annotations by the senior author); see further notes below. In particular, the name has been often allied with *R. sullivantii* in much recent literature (Molano-Flores 2004). These two taxa have similar midwestern ranges.

***Rudbeckia terranigrae* J.J.N. Campbell & Seymour**

2n: ?38 and ?76 (Campbell et al., in prep.).

Notes: see above under description.

***Rudbeckia* aff. *terranigrae*: "*augusta*" ined.**

2n: ?76 (Campbell et al., in prep.).

Notes: see above after description of *Rudbeckia terranigrae*.

UMBROSA-PALUSTRIS SUBGROUP

***Rudbeckia umbrosa* C.L. Boyn. & Beadle**

Rudbeckia fulgida Ait. var. *umbrosa* (C.L. Boynton. & Beadle) Cronq.; type at NY, initially labeled "*tenuifolia* Small ined."

2n: ?76 (Campbell et al., in prep.)

Range: mostly in west-central Appalachian regions (Cumberland Plateau, Ridge & Valley), but extending locally west into the Interior Low Plateaus and east into the Piedmont: Georgia; Tennessee, Kentucky, Ohio, West Virginia (core of range underlined); Virginia, D.C., Maryland.

Habitat: submesic (more or less well-drained) woods in slightly to medium acid soils, often with some calcareous influence, especially on low slopes and stream terraces with partial opening; "low woods and bottoms" (Fernald 1950).

Notes. Collections from some peripheral sections of the range tend to be atypical. A few from sw. Ohio, w. Kentucky and w. Tennessee (KY, NCU, MO, MU, OS) are relatively robust with large basal leaves and long petioles, suggesting transitions from *Rudbeckia umbrosa* towards related species. *Rudbeckia umbrosa* (or *R. fulgida* var. *umbrosa*) has been widely reported from Arkansas, Missouri, and elsewhere in the Midwest (e.g., Deam 1940; Steyermark 1963; Kral 1975; Urbatsch & Cox 2006; Yatskievytch 2006) but apparently just based on confusion with *R. palustris* or *R. sullivantii*.

***Rudbeckia* aff. *palustris*: "*speciosa*" auctores B**

2n: ?76 (Campbell et al., in prep.)

Range: on or near old high terraces and toeslopes of gravelly hills; ?e. Oklahoma, s. Missouri, ?w. Tennessee, ?w. Kentucky, w. Indiana.

Habitat: roadsides, ditches and streamsides, more or less well-drained in most cases but perhaps with some seasonal dampness; on somewhat calcareous to gravelly soils.

Notes. This taxon is tentatively outlined here based on diverse scattered collections, mostly from roadsides, ditches, and streamsides. It may just represent a series of transitions from *Rudbeckia palustris* towards either *R. deamii* or *R. tenax*. Some Indiana localities have also produced collections of typical *R. deamii*. Some collections remain incomplete and have uncertain identification.

***Rudbeckia palustris* Eggert ex C.L. Boynt. & Beadle sensu stricto**

Rudbeckia fulgida Ait. *var. palustris* (Eggert ex C.L. Boynt. & Beadle) Perdue

! *Rudbeckia coryi* Shinners, based on image of type from Texas at BRIT (*V.L. Cory 52412*).

2n: ?38 (Campbell et al., in prep.).

Range: mostly Ozarkian; Texas, Oklahoma, Arkansas, Missouri.

Habitat: mostly in base-rich seeps and fens; "banks of streams, rivers and spring branches, fens and calcareous seeps, bases and ledges of bluffs, and rarely moist depressions of dolomite glades"(Yatskievytch 2006); "damp or wet places" (Fernald 1950); "moist soil, edge of running water" (*Rudbeckia coryi* in Shinners, 1949). Labels on collections confirm that the species is generally associated with slightly alkaline to slightly acid soils.

Notes. As narrowly circumscribed here, *Rudbeckia palustris* is still a variable species, but it appears to be relatively uniform and especially frequent within the Ozark region of Missouri. A collection with aberrant, acuminate-pointed paleae was made in Jefferson Co., Missouri (*Raven 27349* at MO and NY). Plants from further south, especially Texas, tend to have smaller leaves and shorter offsets (including the type of *R. coryi* from Kerr Co.). Especially to the north and east, but even within the core of its range, there has been some confusion with *R. sullivantii* or *R. umbrosa*. It is possible that some intergradation occurs. If plant bases are not collected, determinations are often unreliable. Characters that indicate *R. sullivantii*, as opposed to *R. palustris*, include the following: the largest well-developed basal leaves (strictly basal, not lower cauline) are usually broader (length width ca.

1.5 2 versus 2 3), and more truncate to subcordate (versus usually cuneate to truncate); leaves are typically darker bluish-green (versus paler yellowish-green), thicker and more coarsely hispid; summits of paleae tend to have fewer cilia (or perhaps shorter or more waxed-up or more brittle); and ray florets tend to be longer: mostly 2 3(3.5) cm versus 1 2(3) cm.

***Rudbeckia* aff. *palustris*: "*speciosa*" auctores C**

2n: unknown.

Range: on or near old lacustrine terraces in northern Indiana (Lagrange Co., *C. Deam 55333*, at NY) and northern Illinois (collections from Menard Co. and especially Will Co. at NY, OSU, UGA, US).

Habitat: "common in sandy soil in the wet, sandy, sedge border of the southwest side of North Twin Lake... Lagrange Co., Indiana" (as "*R. palustris*" in Deam, 1940); damp or degraded dolomitic prairie near streams, "infrequent submersed perennial in shoals" (collections from Will Co., Illinois).

Notes. This taxon is tentatively outlined here based on few collections. It may be just an outlying narrow-leaved variant of *Rudbeckia palustris* or perhaps a transition to true *R. speciosa*. The collections are from glaciated terrain, disjunct by about 200 miles from the closest sites with typical *R. palustris* in the Ozarks of southern Missouri. They do, however, overlap with the western edge of the range of typical *R. speciosa*. This taxon might also be confused with *R. sullivantii*, which is well-documented in Will Co., Illinois, but generally quite distinct (Scott & Molano-Flores 2007).

***Rudbeckia chapmanii* C.L. Boynt. & Beadle and allies: "*speciosa*" auctores D**

2n: ?76 (Campbell et al., in prep.)

Range: restricted to the southern Interior Low Plateaus and southern Ridge & Valley; ?n. Mississippi (rare in loess bluffs), n. Alabama, n. Georgia, Tennessee, s. Kentucky.

Habitat: calcareous seeps, springy places and seasonally wet prairies; uncommon to rare in general.

Notes. Types of *chapmanii* (at MO, NY, US, USCH) were collected ca. 1900 by T.P. Cleaveland from Dalton, "Texas Valley" or the "mountains" of Georgia, to be included in the herbarium of A.W. Chapman; some are numbered 169 (plus 2174) and 188 (plus 2195). C.D. Beadle stated (in letter to Britton, 1901, May 14th at NY) that "*R. chapmani* is closest to *R. palustris* from which, however, it is distinguished by its greater size, more numerous rays, smoother stems and especially by the long, slender petioles of both the radical and cauline leaves." The name *R.chapmanii* is tentatively applied here, pending more detailed analysis of the whole *umbrosa-palustris* subgroup. However, the plants grouped here are highly varied in growth form, leaf shape and phenology. Some suggest transitions to *R. palustris*, others to *R. sullivantii* and might be transferred to that taxon (including those from Kentucky). Some plants from Coffee Co., Tennessee, have unusually elongated petiolate leaf-bases and their flowering is late—October to November when cultivated in Fayette Co., Kentucky. Further subdivision of this group of plants may be warranted based on initial morphological assessment. Moreover, their habitats are highly fragmented across their whole range—perhaps leading to ancient general isolation of populations, except for dispersal by megafauna traveling between mineral licks.

***Rudbeckia sullivantii* C.L. Boynt. & Beadle**

Rudbeckia speciosa Wenderoth var. *sullivantii* (C.L. Boynt. & Beadle) B.L. Robins.

2n: 76 (Palmer et al. 2009; Campbell et al., in prep.)

Range: Alleghenies, Mid-western Till Plains and Ozarks, plus scattered disjunctions mostly in or near the southern Interior Low Plateaus: ?Arkansas, ?n. Mississippi (rare in loess bluffs), ?w. Tennessee; Missouri, Illinois, Indiana, Michigan, Ohio (core of range underlined); ?Kentucky, ?West Virginia, ?Pennsylvania, ?New York, ?Vermont (A. Gilman, pers. comm.). It is uncommon to rare across much of its range; some peripheral records may be just from cultivation, especially in the east (as indicated by question marks).

Habitat: in or near fens, calcareous swales, seeps, riparian marshes, damp roadsides and ditches (see also review of Molano-Flores, 2004); "local in moist, wet or springy places about lakes and marshes and along streams and roadsides" (Deam 1940); "swamps, damp shores, etc." (Fernald 1950).

Notes. Some incomplete collections are difficult to distinguish from *Rudbeckia chapmanii* or *R. palustris*, and there may be local intergradation with *R. palustris* in Arkansas, Missouri and Oklahoma. The "*R. speciosa*" of Steyermark (1963) and some other botanists appears to have been based largely on forms of *R. sullivantii*. Steyermark's notes also suggest similarity to *R. tenax*, but that species has not been verified from Missouri or anywhere else west of the Mississippi River. Some plants are distinctly hairier than normal, especially in sites with more hydroxeric character.

A form of *Rudbeckia sullivantii* was selected in Germany over 60 years ago to became the popular ornamental cultivar "Goldsturm" (Jellito 1999; Molano-Flores 2004). It has relatively smooth robust shoots and profuse early inflorescences, but it often suffers from drought and leaf-spotting fungus (especially *Septoria rudbeckiae* Ell. & Holst.). Recently patented selections from Goldsturm that have relatively short compact form and long flowering seasons with less disease are "Early Bird Gold" (Dupont 2009) and "Little Goldstar" (Uebelhart 2011); other named cultivars exist without patents. Analysis of Scott et al. (2007) revealed much overlap within Illinois in genetic markers between wild *R. sullivantii* and Goldsturm, but they found enough difference to recommend that Goldsturm should not be used where gene flow into wild populations might occur. Some collections for herbaria made since 1980 come from naturalized plants of Goldsturm, or their native-versus-escaped status is not clear.

Rudbeckia deamii **S.F. Blake**

Rudbeckia fulgida Ait. var. *deamii* (S.F. Blake) Perdue

2n: ?76 (Campbell et al., in prep.).

Range: Till-plain of central Indiana (Carroll [with type], ?Delaware, ?Huntingdon, Howard, & Warren Cos.) and Interior Low Plateaus of s. Indiana (?Crawford, ?Greene, Harrison, Spencer, Randolph, ?Union & Washington Cos.); "?" indicates data from M. Homoya (pers. comm.), not yet verified here. It has also been reported from s. Illinois and sw. Ohio (Perdue 1957; Urbatsch & Cox 2006; R. Gardner, pers. comm.), but a collection initially identified as *Rudbeckia deamii* from se. Ohio (Highland Co. at NY) now appears closer to "*augusta*" ined. (see above under *R. terranigrae*). A collection from west-central Kentucky (Grayson Co. at NY) suggests a transition from *R. deamii* to "*augusta*" ined. Some of the plants noted above under "*R.* aff. *palustris*; *speciosa* auctores B" suggest transitions to *R. deamii*. Some collections from Missouri (MO, NY) have suggested *R. deamii* but more likely represent atypical hairy forms of *R. sullivantii* or *R. palustris*.

Habitat: mostly along streamsides and roadside ditches; "creek... bank... roadside ditch" (Deam 1940); "wooded ridges and banks of streams" (Fernald 1950).

Notes. This poorly documented species was initially discovered in 1914–17 along creek banks and roadside ditches of central Indiana (Deam 1940). Subsequent work added a disjunct cluster of records from southern Indiana, but there have been few new records from the wild during recent decades (M. Homoya, pers. comm.). There is considerable variation among herbarium collections, and further refinement is needed for its circumscription. *Rudbeckia deamii*, as a variant of "*fulgida*," has become widely grown in gardens since 2000. The plant is usually taller, more long-lasting in its flowers, and more drought tolerant than *R. sullivantii*. It is now much more common in cultivation than in the wild and often extolled by gardeners, especially those from Britain. For example, Klein (2002) noted that "...*Rudbeckia fulgida* var. *deamii* must then be one of the most spiritual of plants. Its flowers are certainly among the most yellow of yellows. Large golden discs—their colour made all the more intense by black, velvety centres—open in huge abundance during early September and continue in succession until the end of October. In some years they go on glowing into the murkiness of November. It is an archetypal 'Indian summer' plant... Given even a modicum of sunshine, flower

follows flower until the entire plant glows. At the height of its glory it is so overpowering that its leaves are almost unnoticed. *Rudbeckia fulgida* var. *sullivantii* 'Goldsturm' is half the height of *R. f. deamii*, at about 18 in [46 cm], with, perhaps, slightly bigger daisies. Both make decent clumps and grow symmetrically from the centre. *R. fulgida* [sensu lato] is a tough plant, brought up in the valleys of eastern North America. Its requirements are simple—decent soil and adequate moisture. It will not die in droughty conditions, but an occasional boost of muck in spring will be welcome."

DISCUSSION

There has been a tendency during recent decades to discount taxonomic divisions within the *Rudbeckia fulgida* complex. This paper aims to revive interest in the taxa recognized by Small (1933) and Fernald (1950) and to outline further complexity that those authors did not recognize. Some North American botanists may resist the idea that generally accepted broad concepts of species should become replaced, where appropriate, by more divisive approaches that claim to be more 'biological'—seeking to define distinct and isolated populations that have not exchanged genes naturally for many generations. We suggest that the situation in *R. fulgida* sensu lato does deserve a more 'biological' approach, leading to a series of difficult questions about species concepts. However, these problems are far less difficult than in some other genera that also appear to have a mix of ancient diploids, early reticulate evolution, later polyploidy, and currently rampant apomixis. One of the most 'nightmarish' cases is *Hieracium* in Europe, as recently addressed by Fehrer et al. (2009). Other intense examples among Asteraceae are *Antennaria* (Bayer 2006) and *Taraxacum* (Majeský et al. 2012). It is notable that all three of those genera contain mostly rosette-forming perennials, often with local vegetative spread and often associated with disturbed ground.

Diversity within the *Rudbeckia fulgida* complex, as well, may eventually be understood in terms of ecological contexts, growth-forms, and genetic processes. The varied biogeographic and edaphic contexts of the habitats for these plants have presumably been a major factor in divergence of these taxa. Most taxa are associated with somewhat disturbed, seasonally damp places in varied types of grassland or thin woodland—seeps, swales, or compacted soils on uplands with poor drainage in winter. However, these sites are often exposed to significant droughts during summer. *Rudbeckia truncata* and *R. missouriensis* are exceptional in their association with more generally xeric sites, although *R. truncata* at least mostly occurs on ledges and rocky hillsides where seepage is significant in the spring. It is hypothesized here that ecological differences between largely hydric versus largely xeric sites have driven the major divisions among taxa. The *fulgida-tenax* subgroup generally occupies intermediate habitats, where disturbance—rather than dryness or dampness—is the major factor that maintains open conditions.

Rudbeckia fulgida itself (sensu stricto), plus varieties, and *R. umbrosa* are largely restricted to somewhat acid soils from Florida and the Atlantic Coastal Plain to Appalachian regions. The other taxa recognized here appear to have radiated from base-rich enclaves of southeastern states (including *R. terranigrae* in the Black Belt and Jackson Prairie) and in more northern regions (with *R. sullivantii* and *R. speciosa* widely scattered over some glacial landscapes). There appears to be a general association of stoloniferous habit with base-rich soils, which could simply reflect the potential for faster growth and spread on more mineral-rich soils. But adaptation to ancient differences in disturbance regime, perhaps involving larger herbivores might also be considered, especially at mineral-rich springs, seeps, and licks. Again, the non-stoloniferous *R. truncata* and *R. missouriensis* are exceptional, usually occurring on drier base-rich soils along cliffs, ledges and rocky hillsides that are less accessible to larger herbivores.

While mechanisms of speciation in *Rudbeckia* remain obscure, the research of Palmer et al. (2009) and others (see Introduction) has suggested that barriers to crossing between some species are strong. Moreover, the potential for local clonal reproduction—through apomixis or stolons—has

presumably allowed proliferation and persistence of distinct taxa within patches of suitable habitat. Hybrids between the three major subgroups of species recognized here have not been clearly demonstrated. But it is likely that some intergradation has occurred among species within each of these subgroups, as noted above under individual taxa. The potential role of polyploidy remains intriguing. Initial estimates of chromosome numbers indicate that several taxa recognized here in the *fulgida* complex do have at least two ploidy levels (J. Campbell, P. Zale, et al., in prep.). *Rudbeckia terranigrae* itself may be largely diploid (with 2n = 38), but the northern population included here, in McNairy Co., Tennessee, appears to be tetraploid. Differences are now being studied in cultivation.

There are clear priorities for further research on the *Rudbeckia fulgida* complex.

(1) Establish more living collections. Differences in vegetative growth and phenology need better description, and there should also be experiments with effects of varied soil types. Also, the potential for hybridization could then be thoroughly investigated.

(2) More chromosome counts. Documentation of differences in ploidy may be critical for understanding species concepts and for relating evolutionary processes to ecological contexts.

(3) More detailed genetic and molecular investigation. The taxonomy presented here could then be tested, based on a better picture of the underlying phylogeny.

(4) More general synthesis of data for a thorough revision. In addition to phylogeny, some aspects of nomenclature will deserve deeper consideration.

New combinations could become appropriate to establish some infraspecific taxa, especially if future work supports a compromise between the post-Fernald (1950) treatments that have culminated in FNA (Urbatsch & Cox 2006) and the more divisive approach promoted in this paper. For example, some botanists might favor three broadly defined species corresponding to the three subgroups outlined above. However, recent research on Asteraceae in general, including genera allied with *Rudbeckia* such as *Echinacea*, *Helianthus, Polymnia*, and *Silphium*, is leading to more acceptance of relatively narrow species concepts in southeastern states (e.g., Estes & Beck 2011; Schilling 2011; Weakley 2012; Peirson et al. 2012; Schilling & Floden 2013, and pers. comm.).

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